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Plant Species Indicators of Physical Environment in Great Lakes Coastal Wetlands

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***ABSTRACT**. Plant taxa identified in 90 U.S. Great Lakes coastal emergent wetlands were evaluated as indicators of physical environment. Canonical correspondence analysis using the 40 most common taxa showed that water depth and tussock height explained the greatest amount of species-environment interaction among ten environmental factors measured as continuous variables (water depth, tussock height, latitude, longitude, and six ground cover categories). Indicator species analysis was used to identify species-environment interactions with categorical variables of soil type (sand, silt, clay, organic) and hydrogeomorphic type (Open-Coast Wetlands, River-Influenced Wetlands, Protected Wetlands). Of the 169 taxa that occurred in a minimum of four study sites and ten plots, 48 were hydrogeomorphic indicators and 90 were soil indicators. Most indicators of Protected Wetlands were bog and fen species which were also organic soil indicators. Protected Wetlands had significantly greater average coefficient of conservatism (C) values than did Open-Coast Wetlands and River-Influenced Wetlands, but average C values did not differ significantly by soil type. Open-Coast and River-Influenced hydrogeomorphic types tended to have sand or silt soils. Clay soils were found primarily in areas with Quaternary glaciolacustrine deposits or clay-rich tills. A fuller understanding of how the physical environment influences plant species distribution will improve our ability to detect the response of wetland vegetation to anthropogenic activities.*

***INDEX WORDS:** Indicator species, soil texture, organic soil, hydrogeomorphic, tussock, coastal wetlands.*

INTRODUCTION

The 5,900 km U.S. shoreline of the Laurentian Great Lakes intercepts a range of climatic, geologic, and hydrologic conditions, so its coastal wetlands occur in a variety of physical environments. Consequently, the flora of Great Lakes coastal wetlands is also diverse, encompassing hundreds of plant species (Geis and Kee 1977, Herdendorf 1992, Minc 1997, Epstein *et al.* 2002).

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Each of the Great Lakes has unique dimensions, climate, and wetland characteristics. Lake Superior is the largest, coldest, and deepest of the Great Lakes, and has an abundance of coastal peatlands (Epstein *et al.* 1997). North-south trending Lake Michigan has drowned river-mouth wetlands along its eastern shore (Wilcox *et al.* 2002) as well as numerous marshes along Green Bay on its western shore (Harris *et al.* 1977). Lake Huron is characterized by shallow, sandy beaches and includes extensive lakebed marshes in Saginaw Bay (Burton *et al.* 2002). Marshes at the western end of Lake Erie, the shallowest and southernmost of the Great Lakes, occupy a postglacial lake plain (Herdendorf 1992). Lake Ontario, the smallest of the Great Lakes by surface area, has numerous lagoons and wetlands protected by barrier beaches along its eastern and southern shorelines (Geis and Kee 1977).

Soils within Great Lakes coastal wetlands have developed from a variety of substrates. The advance and retreat of the Late Wisconsin glaciation deposited materials ranging from gravelly outwash to fine-textured glaciolacustrine deposits in the Great Lakes basin (Fullerton 2004, Fullerton 2005, Fullerton and Richmond 1991, Johnson and Johnston 1995, Richmond and Fullerton 2001a, Richmond and Fullerton 2001b). Organic matter has accumulated in peatlands during post-glacial times, and rivers continue to deposit sandy and silty alluvium.

A wetland's geomorphology influences its vulnerability to hydrologic forces (Wilcox *et al.* 2002). Therefore, any attempt to use plants as indicators of ecological condition must first evaluate the degree to which plant composition reflects the hydrogeomorphology of a wetland. The Great Lakes Environmental Indicators (GLEI) project recognized the importance of coastal wetland hydrogeomorphology in its sample design (Danz *et al.* 2005). The GLEI project categorized wetlands of the U.S. Great Lakes coast into three hydrogeomorphic categories based on definitions by Keough *et al.* (1999): Open-Coast Wetlands, River-Influenced Wetlands, and Protected Wetlands. *Open-Coast Wetlands* are wetlands where emergent plants grow out of shallow lakebed that is relatively exposed to wave action. *River-Influenced Wetlands* include marshes and peatlands that border a river at its confluence with one of the Great Lakes and receive hydrologic inputs from upstream as well as from the lake. *Protected Wetlands* are hydrologically connected with the Great Lakes but "occur landward of a sand barrier, such as an attached spit or beach ridge" that protects them from the full force of wave action (Keough *et al.* 1999). It is *not* an objective of this paper to evaluate the validity of the hydrogeomorphic classes assigned by the GLEI project, which are similar but not identical to hydrogeomorphic classes later used by other Great Lakes groups (e.g., Albert *et al.* 2005). The objective of using the GLEI hydrogeomorphic classes in this manuscript is to determine their association with individual plant species within the context of the greater GLEI sample design.

Individual plant species vary in their responsiveness to the wide array of hydrologic and edaphic conditions that naturally occur in Great Lakes wetlands. Recent research has tested the use of wetland vegetation as an indicator of ecological condition (Albert and Minc 2004, Bertram and Stadler-Salt 1998, Cole 2002, Simon *et al.* 2001, U.S. EPA 2002a, U.S. EPA 2002b, Wilcox *et al.* 2002), but no comprehensive classification exists for individual wetland plant species as indicators of physical environment.

An understanding of individual plant species is a first step in developing indicators of ecological condition because indices based on plant assemblages rely on the cumulative behavior of individual species. An understanding of plant response to the physical environment is also essential to distinguish ecological degradation from inherent ecological variability, because the anthropogenic disturbances that degrade ecological condition are superimposed upon physical environmental gradients. Therefore, the aim of this paper is to evaluate individual plant species as indicators of the physical environment in wetlands of the U.S. Great Lakes coast. Specific objectives are (1) to relate plant species to physical environmental attributes of ground cover, water depth, soil, and location; and (2) to identify plant indicator species of soil and hydrogeomorphic type within U.S. Great Lakes coastal wetlands.

Use of the term "indicator species" follows that of Dufrêne and Legendre (1997) on the association of a species to a particular habitat. This paper does *not* seek to develop indicators of environmental degradation, but see Bourdaghs (2006), Brazner *et al.* (2007), and Frieswyk *et al.* (2007), for more information on linkages with specific stressors.

METHODS

Site Selection and Sampling

Wetland study sites were selected using an objective, stratified random statistical design spanning

TABLE 1. List of study sites. "Lab data" denotes sites for which soil organic matter and particle size data were available. "River or stream" is the name of the largest river or stream that flows into or adjacent to the wetland complex. "Ecoprovince" codes: L = Laurentian Mixed Forest, E = Eastern Broadleaf Forest.

GLEI complex ID	Lab data	Site name	River or stream	Eco-province	State	Lake	Hydro-geomorphic class
1004		Wahbegon Island	Saint Louis River	L	WI	Superior	River
1005	*	Pokegama River	Pokegama River	L	WI	Superior	River
1006		Kimballs Bay	Saint Louis River	L	WI	Superior	River
1008		Hog Island	Unnamed	L	WI	Superior	Open
1009		Nemadji River	Nemadji River	L	WI	Superior	River
1010		Allouez Bay	Bear Creek	L	WI	Superior	Protected
1011		Amnicon River	Amnicon River	L	WI	Superior	River
1012	*	Middle River	Middle River	L	WI	Superior	River
1014		Bois Brule River	Bois Brule River	L	WI	Superior	River
1348		Flag River	Flag River	L	WI	Superior	River
1350		Port Wing	None	L	WI	Superior	Protected
1016		Cranberry River	Cranberry River	L	WI	Superior	River
1017		Bark Bay	Bark River	L	WI	Superior	Protected
1018		Lost Creek	Lost Creek No. 1	L	WI	Superior	Protected
1021		Pikes Creek	Pikes Creek	L	WI	Superior	River
1351		Sioux River Slough	Sioux River	L	WI	Superior	River
1352		Bayview Beach	None	L	WI	Superior	Protected
1024		Chequamegon Bay	Fish Creek	L	WI	Superior	Open
1025	*	Fish Creek	Fish Creek	L	WI	Superior	River
1026	*	Prentice Park	Unnamed	L	WI	Superior	Protected
1353	*	Kakagon River	Kakagon River	L	WI	Superior	Open
1029		Honest John Lake	Denomie Creek	L	WI	Superior	Protected
1039	*	L'Anse Bay	Sixmile Creek	L	MI	Superior	Protected
1040		Lightfoot Bay	None	L	MI	Superior	Protected
1047	*	Au Train River	Au Train River	L	MI	Superior	River
1049	*	Tahquamegon River	Tahquamenon River	L	MI	Superior	River
1050		Munuscong	Munuscong River	L	MI	Huron	Open
1056		Flowers Creek	Flowers Creek	L	MI	Huron	Open
1058		Mackinac Bay	Mackinac Creek	L	MI	Huron	Open
1060	*	Mismer Bay	Steele Creek	L	MI	Huron	Open
1071		Sturgeon River	None	L	MI	Michigan	Protected
1077		Rapid River	Whitefish River	L	MI	Michigan	Open
1356		Ford River Delta	Ford River	L	MI	Michigan	Open
1089	*	Peshtigo River	Peshtigo River	L	WI	Michigan	River
1094	*	Oconto Marsh	Oconto River	L	WI	Michigan	Open
1357		Little Suamico River	Little Suamico River	L	WI	Michigan	Open
1099		Little Tail Point	None	L	WI	Michigan	Open
1359		Sensiba Wildlife Area	Suamico River	L	WI	Michigan	Open
1361		Dead Horse Bay	None	L	WI	Michigan	Open
1102		Peters Marsh	None	L	WI	Michigan	Open
1103		Peats Lake	Duck Creek	L	WI	Michigan	Open
1106		Point au Sauble	Unnamed	L	WI	Michigan	Protected
1109		Toft Point	None	L	WI	Michigan	Protected
1110		Moonlight Bay	None	L	WI	Michigan	Open
1113		Ahnapee River	Ahnappe River	L	WI	Michigan	River
1114		Kewaunee River	Kewaunee River	L	WI	Michigan	River
1116		East Twin River	Twin River	L	WI	Michigan	River
1129		Galien River	Galien River	E	MI	Michigan	River
1130	*	Grand Mere	None	E	MI	Michigan	Protected

TABLE 1. Continued.

GLEI complex ID	Lab data	Site name	River or stream	Eco-province	State	Lake	Hydro-geomorphic class
1132		Black River	Black River	E	MI	Michigan	River
1133		Kalamazoo River	Kalamazoo River	E	MI	Michigan	River
1138		Pigeon River	Pigeon River	E	MI	Michigan	River
1143	*	Mona Lake	Black Creek	E	MI	Michigan	River
1152	*	Big Sable	Big Sable River	L	MI	Michigan	River
1155	*	Arcadia Lake	Bowens Creek	L	MI	Michigan	River
1162	*	Goose Bay	None	L	MI	Michigan	Open
1164		Cecil	None	L	MI	Michigan	Protected
1165	*	Cheboygan Point	None	L	MI	Huron	Protected
1169	*	Misery Bay	None	L	MI	Huron	Open
1170	*	Lake Besser	Thunder Bay River	L	MI	Huron	River
1171		Squaw Bay	None	L	MI	Huron	Protected
1182		Bordeau Road	None	E	MI	Huron	Open
1184		White Feather Creek	White Feather Creek	E	MI	Huron	Open
1187	*	Neuman Road	None	E	MI	Huron	Open
1205	*	Blind Pass	None	E	MI	Huron	Open
1206		Wildfowl Bay	None	E	MI	Huron	Open
1207		Caseville	None	E	MI	Huron	Open
1225		Otter Creek	Otter Creek	E	MI	Erie	River
1226	*	Toledo Beach	Muddy Creek	E	MI	Erie	Protected
1228	*	Bay Creek	Bay Creek	E	MI	Erie	Protected
1229		Little Lake Creek	Little Lake Creek	E	MI	Erie	Protected
1231		Kelly Doty Drain	Kelly Doty Drain	E	MI	Erie	Protected
1238		Magee Marsh	Turtle Creek	E	OH	Erie	Protected
1241	*	Winous Point	Muddy Creek	E	OH	Erie	Protected
1243		Hickory Island	Raccoon Creek	E	OH	Erie	Protected
1254		Huron River	Huron River	E	OH	Erie	River
1260		Presque Isle	None	E	PA	Erie	Protected
1270		Brush Creek	Brush Creek	E	NY	Ontario	River
1275	*	Braddock Bay	Salmon Creek	E	NY	Ontario	Open
1280		Maxwell Bay	Salmon Creek	E	NY	Ontario	Protected
1285	*	Sodus Bay	None	E	NY	Ontario	Protected
1288	*	East Bay	Mudge Creek	E	NY	Ontario	River
1291		Desbrough Park	None	E	NY	Ontario	Protected
1296		Blind Sodus Bay	Blind Sodus Creek	E	NY	Ontario	River
1297		Sterling Creek	Sterling Creek	E	NY	Ontario	Protected
1306		Sage Creek	Sage Creek	E	NY	Ontario	River
1307		Ramona Beach	Snake Creek	E	NY	Ontario	River
1309	*	Deer Creek	Deer Creek	E	NY	Ontario	River
1318	*	Muskellunge Bay	Muskellunge Creek	E	NY	Ontario	Open
1323		Fox Creek	Fox Creek	E	NY	Ontario	River

anthropogenic stressor gradients representing the entire geographic range of the U.S. Great Lakes coast (Danz *et al.* 2005). The 90 wetland complexes selected for study were distributed along the U.S. Great Lakes coast from the western end of Lake Superior to the eastern end of Lake Ontario (Table 1). Sites were classified by hydrogeomorphic type as Open-Coast Wetlands (n = 27), River-Influenced Wetlands (n = 35), or Protected Wetlands (n = 28). Some wetlands had attributes of two or more hydrogeomorphic types and were subdivided accordingly (e.g., complexes 1024–1026, Table 1). Sampling took place from 2001 to 2003 and was restricted to the months of July and August to ensure that most of the vegetation could be identified and peak annual growth was observed. Each wetland was visited once.

Sampling within the selected study sites was done in 1 m × 1 m plots distributed along randomly placed transects within areas mapped as emergent vegetation (sensu Cowardin *et al.* 1979) by national and state wetland inventories along the Great Lakes. Transects were established with a geographic information system (GIS) prior to field campaigns, using a program called Sample (http://www.quantdec.com/sample) to randomize transect placement (Johnston *et al.* in press). Each transect intersected a randomly selected point generated by the Sample program, and was oriented along the perceived water depth gradient, extending from open water to the upland boundary (or to a shrub-dominated wetland zone, if present). Although transects were terminated at the edges of tall shrub-dominated zones, ericaceous shrubs and isolated shrub patches occurring within a predominantly herbaceous plant matrix were included in the sampling. Transect length and target number of sample plots were determined in proportion to the size of the wetland to be sampled (20 plots/60 ha, minimum transect length = 40 m, minimum plots/site = 8). Transect coordinates were uploaded into a handheld global positioning system for use by field crews.

Plot locations were established in the field by dividing each transect into 20 m segments and randomly locating a plot in each segment using a random number table. Within each plot all vascular plant species were identified to the lowest taxonomic division possible (Fassett 1957*,* Voss 1972, Voss 1985, Voss 1996*,* Eggers and Reed 1997*,* Chadde 1998). Large, identifiable non-vascular plants, such as *Chara vulgaris* L. and *Sphagnum* spp., were also given cover estimations. If a plant species could not be identified in the field, it was collected, pressed, and identified in the lab. Percent cover was estimated visually for each taxon according to modified Braun-Blanquet cover class ranges (ASTM 1997): < 1%, 1 to < 5%, 5 to < 25%, 25 to < 50%, 50 to < 75%, 75 to 100%. Prior to data analyses, cover classes were converted to the midpoint percent cover of each class using the algebraic mid-points of the six cover class ranges (0.5, 3.0, 37.5, 62.5, 87.5). Field teams were jointly trained and tested to ensure consistency of visual observations (Kercher *et al.* 2003).

Environmental variables were collected simultaneously with vegetation sampling. Using the same cover class ranges described above, six ground cover categories were recorded: herbaceous litter, autochthonous woody litter, driftwood, bare soil, brown moss (i.e., any non-*Sphagnum* moss species), and open water patches > 10 cm × 10 cm. Other variables measured for each plot were maximum water depth, dominant canopy height, and tussock height. Tussock height was measured by placing a meter stick vertically adjacent to the tallest organic soil mound in a plot, and observing the mound's height from base to summit. Vegetation and environmental variables were characterized at a total of 1,963 plots (average of 22 plots per site).

The soils at each plot were examined to a depth of 30 cm below the litter layer using a soil probe, and assigned to one of the following broad categories: organic, sand, silt, clay. "Organic" soils were those composed of organic soil material (peat or muck) in a histic epipedon (Soil Survey Staff 1999); undecomposed plant litter overlying the soil surface was excluded when making this determination. Only the surface 30 cm was considered, so we did not attempt to discern if soils in the organic category were true histosols. The texture of mineral soils (i.e., sand, silt, clay) was determined by feel using standard field methods (Soil Survey Staff 1951). All field staff were annually trained to perform this hand texturing by co-author Johnston, who is a Professional Soil Scientist certified by the American Society of Agronomy and experienced at wetland soil characterization using both field and laboratory methods (Johnston 2003*;* Johnston *et al.* 1984, 1995, 2001). Field soil characterizations were compared with data on organic matter (weight loss on ignition) and fine particle content (proportion by weight of ashed soil passing through a 63 mm mesh sieve) determined for one-third of our sites by the GLEI group studying invertebrate indicators (Valerie Brady and Lucinda Johnson, Natural Resources Research Institute, University of Minnesota, Duluth personal communication).

The Interagency Taxonomic Information System (http://www.itis.usda.gov) was used as the ultimate taxonomic authority, and the USDA Plants Database (USDA NRCS 2004) was used for species symbol codes. Values for "coefficient of conservatism" (*C* value), a ranking system developed by Swink and Wilhelm (1969) to indicate a plant's fidelity to "remnant natural plant communities," were obtained from the Michigan Natural Heritage Program (Herman *et al.* 2001). A *C* value of 0 signifies no confidence that a species came from a natural community (e.g., *Phalaris, Phragmites*), whereas a value of 10 signifies a plant that almost certainly comes from an undegraded remnant natural plant community; non-native species receive no *C* values.

Although other Great Lake states have also developed coefficient of conservatism lists, Michigan values (Herman *et al.* 2001) were used for simplicity because 40% of the study sites were in Michigan and because Michigan spans most of the north-south gradient of the Great Lakes.

Statistical and Geographical Analysis

Indicator species analysis (ISA) was used to identify plant species indicative of physical environment (Dufrêne and Legendre 1997). ISA is a computational method that uses categories defined *a priori* (e.g., environmental variable categories), and determines the faithfulness of occurrence of a species to a particular category based on species frequency and abundance. In Dufrêne and Legendre's terminology, the "indicator value" of a species in a given category is calculated as:

$$IV_{kj} = 100(RA_{kj} \times RF_{kj}) \qquad (1)$$

where RF_{kj} is relative frequency, the proportion of sample units (e.g., plots) in group k that contain species j; and RA_{kj} is the relative abundance of species j in group k. The RA_{kj} term is computed as average abundance of a species in a category of plots (e.g., plots with organic soil) divided by the average abundance of that species in all plots. The RA_{kj} term measures exclusiveness, the concentration of abundance into a particular group, whereas the RF_{kj} term measures the faithfulness or constancy of presence in a particular group; *both* values must be relatively high for the species to be a significant indicator species (McKune and Grace 2002). The statistical significance of the computed IV_{kj} values was tested for each species by Monte Carlo simulations (1,000 randomizations). A significance threshold of $p < 0.05$ was used to identify hydrogeomorphic indicator species, but a more restrictive significance threshold of $p < 0.01$ was used to identify soil indicator species due to the large number of plots (n = 1,963) included in the soil ISA. All calculations were done using the PC-ORD software package (McCune and Mefford 1999). Details of the indicator species methodology and examples of its application are described by McCune and Grace (2002).

Indicator species analyses were performed for the two types of physical variables at two scales: hydrogeomorphic type at the site scale (n = 90: Table 1), and soil type at the plot scale (n = 1,963: Table 2). The ISA was performed using 169 candidate taxa which met the criteria of: (1) occurring in a minimum of four sites and ten plots; and (2) being identified to species, with the exception of three non-vascular genera (*Azolla* sp., *Riccia* sp., *Sphagnum* sp.). The same 169 candidate taxa were used for both soil and hydrogeomorphic indicator species analyses, but their cover data were aggregated differently: species cover per plot was used in the soil ISA, whereas mean species cover per site was used in the hydrogeomorphic ISA.

Canonical correspondence analysis (CCA: ter Braak 1986, Palmer 1993) was used to relate common species, those which occurred in more than 20 of the 90 sites, to ten environmental characteristics (water depth, tussock height, latitude, longitude, and the six ground cover categories) measured at the plot scale. Axis scores were centered and standardized to unit variance, and axes scaled to optimize representation of species. The CCA calculations were done using PC-ORD (McCune and Mefford 1999).

A species-area curve (Hill *et al.* 1994) was constructed to show the increasing number of species observed as sample plots were successively pooled. Computations were done using the PRIMER software package (Clarke and Gorley 2006), using random permutation to enter samples in random order 999 times. Other statistical analyses were performed with SAS/STAT® 9.0 software (SAS Institute, Cary NC).

Digital versions of Quaternary geology maps for the Great Lakes (Fullerton 2004, 2005; Fullerton and Richmond 1991; Richmond and Fullerton 2001a, 2001b) were obtained from the U.S. Geological Survey Geologic Investigations Series Online (http://pubs.usgs.gov/products/maps/i-maps.html) and used to map Late Wisconsin glaciolacustrine silt and clay deposits using ArcMap™ 9.1 (ESRI, Redlands CA). GIS methods are detailed by Johnston and colleagues (in press).

TABLE 2. Number of sample plots by soil type and lake.

Lake	Organic	Clay	Silt	Sand	Total by lake
Superior	265	50	117	49	481
Huron	22	17	79	185	303
Michigan	493	24	30	200	747
Erie	19	112	60	19	210
Ontario	188	31	2	1	222
Total by soil	987	234	288	454	1,963

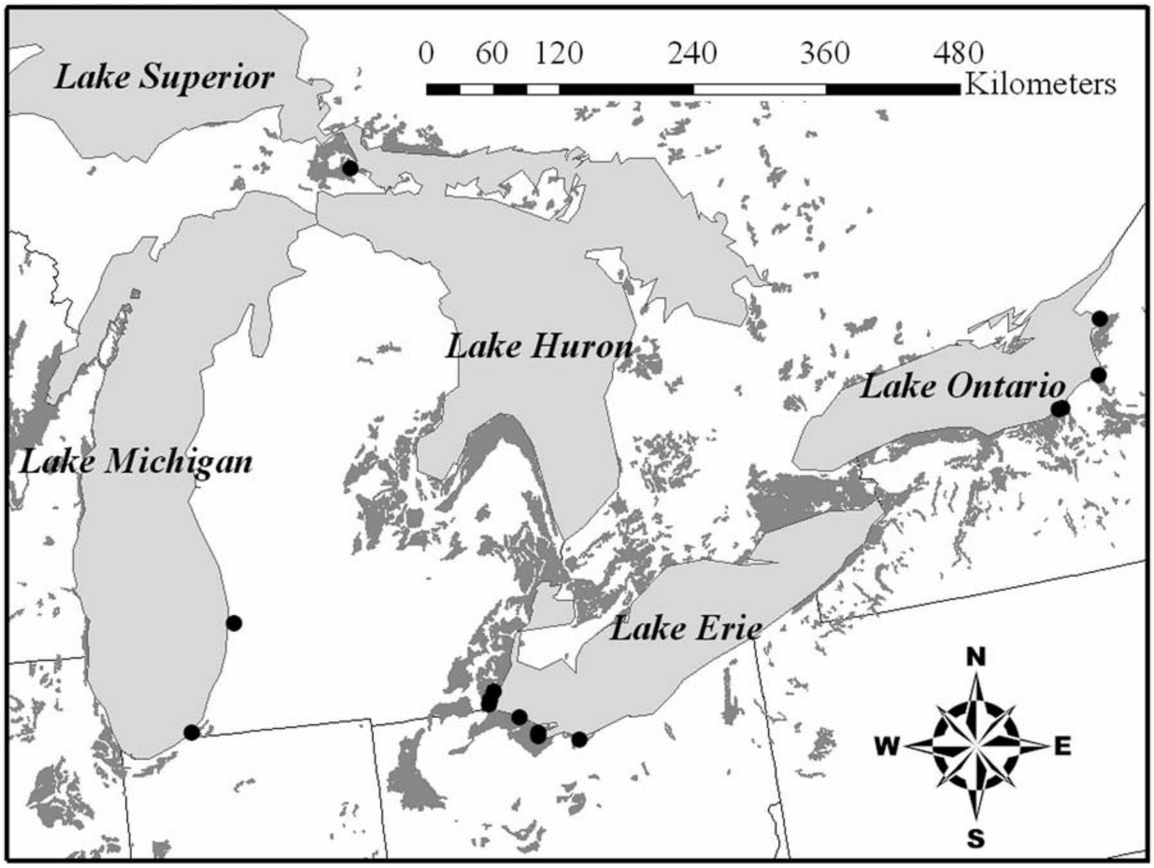

FIG. 1. Study sites (•) in the lower Great Lakes observed to have clay soils, plotted on a map of glaciolacustrine clay deposits.

RESULTS

Sample Characteristics

In all, 1,963 plots were sampled in the 90 wetlands studied. Half of the plots sampled (987 of 1,963 plots) were classified as organic, of which the majority was in Lakes Superior and Michigan (Table 2). The other half of the plots were mineral soils of sand, silt, or clay texture, respectively constituting 23%, 15%, and 12% of the total number of plots. Lakes Michigan and Huron had the most sand plots, and Lake Superior had the most silt plots. Lake Ontario contained primarily organic and clay soil plots.

Clay soils occurred in seven of the ten Lake Erie study sites and nine of the 21 sites on western Lake Superior. Other study sites with clay soils occurred on eastern Lake Ontario, southern Lake Michigan, and the Munuscong site on Lake Huron. With the exception of the Kalamazoo site on the eastern shore of Lake Michigan (complex 1133), all of the sites in which we found clay soils occurred on glaciolacustrine sediments deposited during the Late Wisconsin period, as mapped by the U.S. Geological Survey (Fig. 1).

Field determination of soil classes was corroborated by laboratory data. Soils determined in the field to be "sand" had fine particle contents averaging only 3.5%, as compared with 20.3% for field-determined silt or clay soils. Soils determined in the field to be "organic" had an average organic matter content of 39.5%, as compared with only 3.2% for soils determined in the field to be sand, silt, or clay (i.e., non-organic). Soil horizons > 20–35% organic matter are considered to be organic by soil taxonomists (Soil Survey Staff 1999).

The species-area curve computed for the dataset showed that a random sample of only 196 plots, one-tenth the number actually sampled, would have yielded 156 ± 3.4 of the 169 taxa which were ultimately used in the ISA. This analysis illustrates that the 1,963 plot sample size was sufficiently large to more than adequately characterize plant species diversity.

Species Indicators of Soil Type

Based on the Monte Carlo simulations of the ISA, 90 of the 169 candidate taxa were significantly ($p < 0.01$) associated with a particular soil type (Table 3). A value close to 100 for RA_{kj} denotes a species that is nearly always associated with that soil type. For example, the value of 99% for large cranberry (*Vaccinium macrocarpon*) means that 99% of the 47 plots in which it occurred had organic soil. A species with a lower RA_{kj} value could still be a significant indicator of soil type, particularly if the total number of plots of occurrence was large. For example, wooly-fruit sedge (*Carex lasiocarpa*) was an indicator of organic soil, but only 47% of the 370 plots in which it occurred had organic soil. Organic soil was the modal soil type for wooly-fruit sedge, but the species also occurred frequently on sandy soils.

Within our dataset, the majority of the taxa that were significant soil indicators occurred in both the Laurentian Mixed Forest and the Eastern Broadleaf Forest ecoprovinces. Nine soil indicators occurred only in the Eastern Broadleaf Forest ecoprovince, 24 soil indicators occurred only in the Laurentian Mixed Forest ecoprovince, and the remainder (57 taxa) occurred in both (Table 3). These occurrences represent the ecoprovince distribution only within the data that we collected, however, and are not equivalent to plant range maps.

There were 28 organic soil indicator species, of which more than half were taxa typically associated with bogs and poor fens: *Andromeda polifolia, Carex lasiocarpa, Chamaedaphne calyculata, Drosera rotundifolia, Menyanthes trifoliata, Myrica gale, Pogonia ophioglossoides, Rhynchospora alba, Rhynchospora fusca, Salix pedicellaris, Sarracenia purpurea, Solidago uliginosa, Sphagnum* sp., *Triadenum fraseri, Utricularia intermedia,* and the two *Vaccinium* species. These bog and fen taxa are more common in northern wetlands, and ten of the organic soil indicators occurred exclusively in the Laurentian Mixed Forest ecoprovince within our dataset. All of the bog and fen taxa except *Solidago uliginosa* had C values ≥ 6, indicating a strong fidelity to remnant natural plant communities. Organic soil indicator species that had low C values included stinging nettle (*Urtica dioica,* $C = 1$) and the invasive exotics frogbit (*Hydrocharis morsus-ranae*) and hybrid cattail (*Typha* x *glauca*, $C = 0$).

The 26 sand indicator species included 12 species of true rushes (*Juncus* spp.), spikerushes (*Eleocharis* spp.), and bulrushes (*Schoenoplectus* spp.). Other graminoid monocots among the sand indicator species were four grasses (*Agrostis hyemalis, Dichanthelium acuminatum, Glyceria striata, Muhlenbergia glomerata*), two sedges (*Carex hystericina, C. viridula*), and seaside arrowgrass (*Triglochin maritimum*). Nine of the sand indicator species occurred only in the Laurentian Mixed Forest ecoprovince within our dataset.

The 19 species that were indicators of silty soils included most of the submerged and rooted-floating aquatic species on the soil indicators list: *Chara vulgaris, Elodea canadensis, Myriophyllum sibiricum, Najas flexilis, Nuphar lutea, Nymphaea odorata, Potamogeton friesii,* and *Stuckenia filiformis*. Other silt soil indicators tended to be species capable of rooting in subaqueous soils (i.e., marshes), such as *Equisetum fluviatile, Schoenoplectus subterminalis, Schoenoplectus tabernaemontani, Sparganium eurycarpum, Zizania aquatica,* and the two *Sagittaria* species.

The clay indicators group included all six of the free-floating plant taxa that were soil indicators: *Azolla* sp., *Riccia* sp., *Ricciocarpos natans, Spirodela polyrrhiza, Lemna minor,* and *L. trisulca*. These tiny plants were not rooted in the substrate, and almost always occurred beneath the protective overstory of taller emergents, such as *Phragmites australis* or *Typha* spp. (Fig. 2). Two common invasive species, reed canary grass (*Phalaris arundinacea*) and narrowleaf cattail (*Typha angustifolia*), were also significant indicator species for clay soils.

The C values for species that were soil indicators spanned the range of possible values (Table 3). There was no significant difference in average C values by soil type (ANOVA, $F = 0.59$, $p = 0.623$), implying that remnant natural plant communities are not restricted to any particular soil type.

Species Indicators of Hydrogeomorphic Type

Of the 169 candidate taxa considered in the ISA, 48 were significant ($p < 0.05$) indicators of hydrogeomorphic type (Table 3). Two-thirds of the hydrogeomorphic indicator species were also soil indicators.

The twelve indicators for Protected Wetlands were primarily species associated with bogs and fens, and most were also indicators of organic soil. The three Protected Wetland indicators that were

TABLE 3. Indicator species for soil and hydrogeomorphic type. USDA symbols provided for common plant species used in CCA analysis. C = coefficient of conservatism values (Herman* et al. *2001). RA_{kj} = relative abundance in group (see equation 1); when two numbers are given, the first is for soil indicator group and the second is for geomorphic indicator group. "Province" = ecoprovince of occurrence within the dataset used; L = Laurentian Mixed Forest, E = Eastern Broadleaf Forest.

Plant species	USDA symbol	*C*	Total plots of occurrence	Soil type indicated	Geomorphic type indicated	RA_{kj}, %	Province
Acorus calamus		6	40	–	river	89	LE
Agalinis purpurea		7	12	–	open	99	LE
Agrostis hyemalis		4	15	sand	–	87	L
Andromeda polifolia var. *glaucophylla*		10	147	organic	protected	65, 91	LE
Argentina anserina		5	30	sand	open	87, 81	LE
Azolla sp.		nr	24	clay	–	74	E
Calamagrostis canadensis	CACA4	3	433	organic	open	45, 55	LE
Calla palustris		10	95	clay	river	60, 68	LE
Campanula aparinoides	CAAP2	7	248	–	open	61	LE
Carex comosa	CACO8	5	80	silt	open	53, 81	LE
Carex hystericina		3	27	sand	–	89	L
Carex lacustris	CALA16	6	246	–	river	65	LE
Carex lasiocarpa var. *americana*	CALAA	8	370	organic	–	47	LE
Carex scoparia		4	22	–	open	100	L
Carex utriculata		5	62	silt	river	58, 71	L
Carex viridula		4	23	sand	open	91, 87	LE
Cephalanthus occidentalis		7	21	–	protected	98	E
Ceratophyllum demersum	CEDE4	1	74	clay	–	56	LE
Chamaedaphne calyculata		8	113	organic	protected	85, 80	LE
Chara vulgaris		nr	61	silt	open	67, 61	LE
Cirsium muticum		6	38	–	open	84	LE
Cladium mariscoides		10	89	organic	protected	84, 93	L
Comarum palustre	COPA28	7	178	silt	river	47, 77	LE
Cornus sericea spp. *sericea*		2	19	–	river	93	LE
Dasiphora floribunda		10	45	sand	–	82	L
Dichanthelium acuminatum var. *lindheimeri*		8	17	sand	–	100	LE
Drosera rotundifolia		6	94	organic	–	97	L
Eleocharis acicularis		7	15	sand	open	96, 100	LE
Eleocharis elliptica		6	34	–	protected	65	LE
Eleocharis erythropoda	ELER	4	112	sand	open	73, 81	LE
Eleocharis palustris	ELPA3	5	81	sand	–	64	LE
Eleocharis quinqueflora		10	10	sand	–	100	L
Elodea canadensis	ELCA7	1	48	silt	–	86	LE
Epilobium coloratum		3	16	silt	–	67	L
Equisetum fluviatile	EQFL	7	168	silt	–	74	L
Eupatorium perfoliatum	EUPE3	4	73	sand	open	70, 75	LE
Euthamia graminifolia		3	52	sand	open	83, 67	LE
Galium tinctorium		5	70	clay	–	60	LE
Glyceria striata		4	15	sand	–	90	LE
Hibiscus moscheutos		7	40	clay	protected	52, 91	E
Hydrocharis morsus–ranae		0	73	organic	–	60	E
Juncus alpinoarticulatus		5	13	sand	–	98	LE
Juncus balticus var. *littoralis*		4	50	sand	open	98, 62	LE
Juncus brevicaudatus		8	18	sand	–	100	L
Juncus dudleyi		1	36	sand	open	95, 97	L
Juncus nodosus	JUNO2	5	117	sand	open	84, 89	LE
Juncus pelocarpus		8	37	sand	open	67, 94	LE
Lemna minor	LEMI3	5	298	clay	–	79	LE
Lemna trisulca		6	54	clay	–	74	LE

TABLE 3. Continued.

Plant species	USDA symbol	*C*	Total plots of occurrence	Soil type indicated	Geomorphic type indicated	RA_{kj}, %	Province
Lysimachia thyrsiflora	LYTH2	6	175	organic	–	60	LE
Menyanthes trifoliata		8	77	organic	protected	96, 72	L
Muhlenbergia glomerata		10	28	sand	–	86	L
Myrica gale	MYGA	6	227	organic	–	56	LE
Myriophyllum sibiricum		10	21	silt	–	58	LE
Najas flexilis		5	21	silt	–	64	LE
Nelumbo lutea		8	28	clay	–	65	E
Nuphar lutea ssp. *variegata*		7	36	silt	–	86	LE
Nymphaea odorata		6	84	silt	–	52	LE
Peltandra virginica		6	108	organic	river	55, 86	E
Phalaris arundinacea	PHAR3	0	212	clay	–	37	LE
Pogonia ophioglossoides		10	31	organic	–	98	L
Polygonum hydropiperoides		5	35	clay	–	78	LE
Polygonum sagittatum		5	29	clay	–	61	LE
Pontederia cordata		8	41	clay	–	52	LE
Potamogeton friesii		6	29	silt	–	95	LE
Proserpinaca palustris		6	12	sand	–	100	LE
Rhynchospora alba		6	79	organic	–	80	L
Rhynchospora fusca		7	30	organic	–	100	L
Riccia sp.		nr	22	clay	–	66	E
Ricciocarpus natans		nr	26	clay	–	92	LE
Rosa palustris		5	11	organic	–	100	LE
Sagittaria graminea		10	50	silt	–	83	LE
Sagittaria latifolia	SALA2	1	268	silt	–	58	LE
Salix discolor		1	29	–	river	87	LE
Salix pedicellaris		8	60	organic	–	69	LE
Salix petiolaris		1	39	–	open	100	LE
Sarracenia purpurea		10	102	organic	protected	53, 96	L
Schoenoplectus acutus var. *acutus*		5	39	sand	–	67	LE
Schoenoplectus pungens var. *pungens*		5	134	sand	open	81, 98	LE
Schoenoplectus subterminalis		8	21	silt	open	42, 95	L
Schoenoplectus tabernaemontani	SCTA2	4	267	silt	open	46, 47	LE
Scutellaria galericulata	SCGA	5	154	organic	river	51, 64	LE
Solidago canadensis		1	22	–	open	84	LE
Solidago uliginosa		4	14	organic	–	100	L
Sonchus arvensis		0	24	–	open	74	LE
Sparganium eurycarpum	SPEU	5	295	silt	river	43, 52	LE
Sphagnum sp.		nr	123	organic	protected	82, 81	L
Spirodela polyrrhiza		6	104	clay	–	78	LE
Stuckenia filiformis		7	11	silt	open	71, 100	E
Symphyotrichum boreale		9	39	sand	protected	86, 100	L
Thelypteris palustris	THPA	2	101	organic	–	100	LE
Thuja occidentalis		4	36	sand	–	83	LE
Triadenum fraseri		6	45	organic	protected	76, 64	L
Triadenum virginicum		10	37	organic	–	97	E
Triglochin maritimum		8	14	sand	–	92	LE
Typha angustifolia	TYAN	0	221	clay	–	54	LE
Typha latifolia	TYLA	1	165	–	river	57	LE
Typha x *glauca*	TYGL	0	214	organic	–	42	LE
Urtica dioica		1	127	organic	–	51	LE
Utricularia intermedia		10	48	organic	–	98	LE
Utricularia macrorhiza	UTMA	6	101	clay	–	67	LE
Vaccinium macrocarpon		8	47	organic	–	99	LE
Vaccinium oxycoccos		8	82	organic	protected	81, 84	LE
Zizania aquatica		9	21	silt	river	97, 99	L

FIG. 2. Photo of the free-floating liverwort* Ricciocarpos natans *beneath a canopy of* Typha *at the Point au Sauble study site (complex 1106). An individual plant is circled.

not associated with bogs or fens were elliptic spikerush (*Eleocharis elliptica*), buttonbush (*Cephalanthus occidentalis*), and rose-mallow (*Hibiscus moscheutos*).

Twenty-four species were indicators of Open-Coast Wetlands. About half of the Open-Coast Wetland species were sedges or rushes: *Carex comosa, C. scoparia, C. viridula, C. vulgaris, Eleocharis acicularis, E. erythropoda, Juncus balticus, J. dudleyi, J. nodosus, J. pelocarpus, Schoenoplectus pungens, S. subterminalis,* and *S. tabernaemontani*. Of the Open-Coast Wetland indicators that were also soil indicators, eleven were sand indicators, five were silt indicators, and one was an organic soil indicator.

Despite the abundance of River-Influenced Wetland sites sampled, only twelve plant species were indicators of that hydrogeomorphic type. Silt was the most common soil type when plants were indicators of both a soil type and the River-Influenced hydrogeomorphic type. One-third of the River-Influenced indicators were common species, those occurring within more than 20 sites: *Carex lacustris, Comarum palustre, Scutellaria galericulata*, and *Sparganium eurycarpum*.

There was a significant effect of hydrogeomorphic type on average *C* values of indicator species (ANOVA, $F = 10.3$, $p = 0.0002$). Average *C* values were significantly greater for Protected Wetlands than for wetlands in the other two hydrogeomorphic types (Table 4), implying that Protected Wetlands tend to contain disproportionately more remnant natural plant communities than do Open-Coast and River-Influenced Wetlands.

Canonical Correspondence Analysis

Only 40 species occurred within more than 20 study sites, referred to hereinafter as the common

TABLE 4. Mean C values of hydrogeomorphic indicator species, by hydrogeomorphic type. Means with the same superscript letter are not significantly different.

Geomorphic type	C Average (±S.D.)
Protected	8.09 (1.5)[a]
River-influenced	5.25 (2.8)[b]
Open-coast	4.48 (2.3)[b]

plants. Most of the common plants had a growth habit of graminoid or forb/herb, consistent with the project's focus on emergent wetlands, but the list also included several submergent aquatics, one free-floating aquatic (*Lemna minor*), and two shrub species (*Alnus incana* ssp. *rugosa* and *Myrica gale*). Except for a horsetail (*Equisetum fluviatile*) and a fern (*Thelypteris palustris*), all of the common species were flowering plants. There was only one common annual, jewelweed (*Impatiens capensis*). Although the common plant list contains many dominant species (Frieswyk *et al.* 2007), it also includes subcanopy plants such as marsh bellflower (*Campanula aparinoides*) and bulb waterhemlock (*Cicuta bulbifera*) which occur at multiple wetland sites but have low cover.

The CCA analysis comparing the 40 common species to ten site environmental characteristics yielded three canonical correspondence axes that represented water depth, tussock height, and herbaceous litter cover, respectively (Table 5). A graph of species relative to the first two canonical axes, water depth and tussock height, separated the four submergent and floating aquatic species (*Ceratophyllum demersum, Elodea canadensis, Lemna minor,* and *Utricularia macrorhiza*) on the left side of the CCA plot from emergent species in the center and right side of the plot (Fig. 3). Average water depth of plots containing these four species ranged from 37 cm for duckweed (*Lemna*) to 48 cm for coontail (*Ceratophyllum*). A group in the middle of the graph contained emergent wetland species with average water depths from 13 to 19 cm: *Cicuta bulbifera, Equisetum fluviatile, Polygonum amphibium, Sagittaria latifolia, Schoenoplectus tabernaemontani, Typha angustifolia*, and *T. latifolia.*

Tussock sedge (*Carex stricta*) fell at extreme CCA values for both water depth (very shallow water) and tussock height (tallest tussocks). Average tussock height for plots containing *C. stricta* was 18.8 cm. The extreme low value for the tussock height axis was represented by jointed rush (*Juncus nodosus*), which grew out of bare soil with no tussocks. Other species with low values for the tussock height axis included *Eleocharis erythropoda, Eupatorium perfoliatum, Leersia oryzoides,* and *Phragmites australis.*

TABLE 5. Axis summary statistics and regression with environmental variables (standardized canonical coefficients) produced by canonical correspondence analysis.

Variable	Axis 1	Axis 2	Axis 3
Water depth	**–0.713**	0.562	–0.392
Tussock height	0.352	**0.873**	0.355
Site longitude	0.026	0.045	0.014
Site latitude	–0.011	–0.006	0.087
Herbaceous litter cover	0.212	0.104	**–0.746**
Autochthonous woody litter cover	0.044	0.109	–0.03
Driftwood cover	–0.033	–0.007	0.058
Bare soil cover	0.015	–0.230	0.458
Brown moss cover	0.007	–0.007	–0.162
Open water cover	–0.098	0.019	0.031
Eigenvalue	0.471	0.255	0.176
Variance in species data			
% of variance explained	2.7	1.5	1.0
Cumulative % explained	2.7	4.1	5.1
Pearson Correlation, Spp–Envt	0.780	0.646	0.520
Kendall (Rank) Corr., Spp-Envt	0.559	0.380	0.332

DISCUSSION

Geomorphology and soils provide important environmental templates for the establishment of wetland vegetation (Meeker 1996, Johnston 2003, DeSteven and Toner 2004). Geomorphic settings influence wetland hydrologic regimes, substrates, and chemistry (Brinson 1993, Bedford 1996, Kirkman *et al.* 1998, Johnston *et al.* 2001). Differences in soil particle size and organic matter content can influence plant germination (Keddy and Constabel 1986, Wilson and Keddy 1986), which may ultimately influence plant community composition. Individual plant species are thus useful indicators of physical environmental factors at plot (water depth, soil) and site (hydrogeomorphic type) scales.

Properties of Indicator Species Analysis

The ISA method has helped other authors relate plant distributions to environmental conditions in

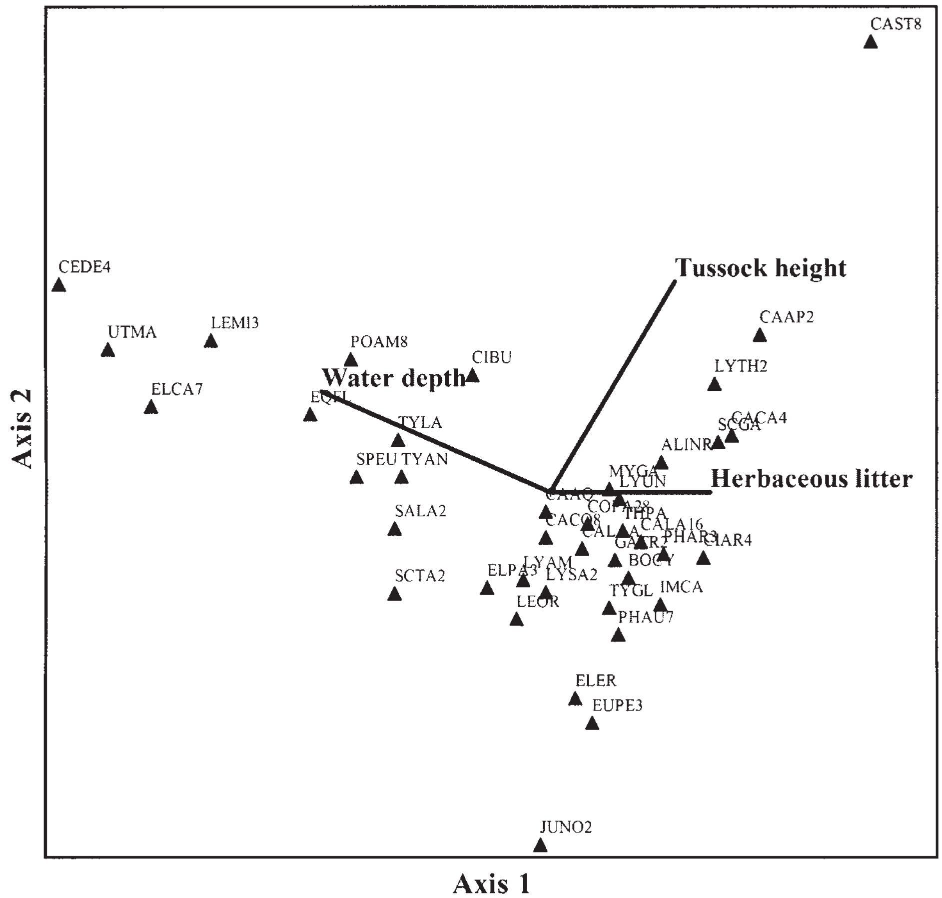

FIG. 3. Ordination of common species in environment space, as defined by CCA, using LC scores. ALINR* = Alnus incana*, BOCY* = Boehmeria cylindrica*, CAAQ* = Carex aquatilis*, CAST8* = Carex stricta*, CIBU* = Cicuta bulbifera*, CIAR4* = Cirsium arvense*, GATR2* = Galium trifidum*, IMCA* = Impatiens capensis*, LEOR* = Leersia oryzoides*, LYAM* = Lycopus americanus*, LYUN* = Lycopus uniflorus*, LYSA2* = Lythrum salicaria*, POAM8* = Polygonum amphibium*, PHAU7* = Phragmites australis*; other species codes listed in Table 3. The biplot overlay shows vectors related to the two strongest environmental variables.

recent studies of wetland vegetation (Baker and Wiley 2004, DeSteven and Toner 2004, King *et al.* 2004), but its properties should be understood in interpreting results. Indicator species must have relatively high values for *both* relative frequency (RF_{kj}) and relative abundance (RA_{kj}) in a category (McCune and Grace 2002), which eliminated some candidate species from being indicators. For example, beaked sedge (*Carex rostrata*) had a high RA_{kj} in organic soils (77%), but its relative frequency in organic soils was only 2% (i.e., it occurred in only 2% of the 987 organic soil plots), so it was not a significant soil indicator species. Conversely, a common species like reed canary grass with an RA_{kj} value for clay soils of only 37% (Table 3) was a soil indicator species due to its high relative frequency in clay soils of 18% (i.e., occurring in 18% of the 234 clay plots). Identification of an indicator species does not preclude that species from occurring in other groups, it only means that the species has a significant preference for the modal group. The combination of the two attributes, RF_{kj} and RA_{kj}, makes practical sense for development of Great Lakes environmental indicators because it ensures that: (1) a species is likely to be encountered in a Great Lakes coastal wetland (RF_{kj}) and (2) once encountered, it has a high statistical probability of association with the environmental characteristic for which it is an indicator (RA_{kj}). If greater indicator exclusivity is desired, the values in Table 3 could be used to impose a higher RA_{kj} threshold to limit indicators to those that are nearly always associated with a particular environmental characteristic (e.g., occurring in clay soils > 70% of the time).

None of the species that were *significant* indicator species based on the Monte Carlo analysis achieved *perfect* indication, meaning that the presence of a species points to a particular group without error (McCune and Grace 2002). In fact, the species that was the best soil indicator species achieved only 32% of perfect indication based on its RF_{kj} and RA_{kj} scores. This low numerical value is largely a function of the rigorous test imposed by our very large species pool and number of sample units, and does not diminish an individual species' significance or utility as an indicator.

The ISA method uses pre-defined categories, and a species may be an indicator of one and only one category. The hydrogeomorphic and soil classifications that we utilized included three and four categories, respectively. We intentionally used just a few categories that could be consistently applied, so as to minimize potential classification error. In some cases, our classes may have been too narrow. For example, some species may be indicators of fine-textured soils without a preference for silt or clay, which would be revealed by combining soil and clay plots into a single fine-textured category. In other cases, our classes may have been too broad, and subdividing them into more categories might have been more ecologically meaningful. For example, subdividing the organic soil class into soil with acid versus circumneutral pH might reduce the breadth of conditions encompassed within this class. This research did not test alternative classification schemes, but such work could be the subject of future studies.

The ISA method relies on the dataset used for the computation, and therefore the environmental preferences of indicator species listed in Table 3 may differ under conditions not represented by this dataset. For example, northern white-cedar (*Thuja occidentalis*) was an indicator of sandy soils in our study of coastal wetlands, but inland cedar swamps are usually associated with organic soils (Johnston 1990). Our results should not be extrapolated to areas other than Great Lakes coastal wetlands.

Soil and Hydrogeomorphic Indicator Species

There was a tendency for different plant life forms to be associated with the different soil types. For example, submerged aquatic species tended to be silt indicators, free-floating plants tended to be clay indicators, and sand indicators tended to have graminoid forms (although the reverse was not true, because graminoid plants were indicators of multiple soil types). These associations may be caused by a single driver such as the influence of a site's wave energy on its soil particle size *and* plant life forms. Sandy soils often occur in erosive coastal environments with substantial wave action, conditions which are tolerated by graminoids in the *Cyperaceae* and *Juncaceae* having stiff tissues and strong rooting systems. Silty soils tend to occur in more depositional environments, and are often associated with quiescent conditions that can sustain more fragile plants such as submerged aquatics. Clay soils persist under quiescent conditions that are capable of harboring free-floating plants. Thus, soil type may actually be a surrogate indicator for the wave energy of a site.

At some wetland sites, however, soil texture is a relict of conditions that occurred thousands of years in the past, and is unrelated to current fluvial action. Sandy wetland soils may be relicts of glaciofluvial deposition (Johnston *et al.* 1984), which is why the protected wetland indicator species northern bog aster (*Symphyotrichum boreale*) was also a sand indicator. Clay soils within our study sites were relicts of glaciolacustrine deposition (Fig. 1) or clay-rich glacial tills (Johnson and Johnston 1995). Clay soils generally do not signify active sedimentation, because eroded clays are transported in suspension long distances beyond coastal wetlands into deeper portions of the Great Lakes (Hawley and Niester 1993, Shuter *et al.* 1978, Thomas *et al.* 2006). Thus, soil texture can be used to make some inferences about the fluvial energetics of a wetland site, but that interpretation must be tempered by knowledge of a site's geologic origins.

Because free-floating plants are not rooted in the substrate, we were surprised that six free-floating species were indicators of clay soils. One possible explanation already noted is the quiescent conditions that would allow both clay soils and free-floating plants to persist in a wetland. Another possible explanation is an indirect relationship with clay particles suspended in the water column. Fine soil particles are rich in phosphorus (Johnston

1991, Bridgham *et al.* 2001), so there may have been a fertilization effect that promoted these free-floating species. Using ISA, the free-floating plant duckweed was found to be a highly significant indicator of anthropogenic fertilization in Everglades's wetlands (King *et al.* 2004).

Hydrogeomorphic indicators were strongly related to soil indicators in Protected Wetlands, but were less so in Open-Coast and River-Influenced Wetlands. Two-thirds of the Protected Wetland indicator species were also indicators of organic soils, which is consistent with the original definition of this hydrogeomorphic type by Keough and coworkers (1999). Open-Coast and River-Influenced hydrogeomorphic types tended to have sand and silt soils, respectively, which is consistent with the wave erosion and alluvial deposition that occurs under those hydrogeomorphic conditions.

The analysis of hydrogeomorphic indicators provided quantitative insights into plant-environment relationships which were helpful in interpreting *C* value designations. Indicator species of Protected Wetlands had significantly higher average *C* values than did indicator species of River-Influenced or Open-Coast Wetlands, a finding similar to that of Bourdaghs (2006) for wetlands in the Laurentian Mixed Forest province. Many of the plants that were indicators of Protected Wetlands were distinctive bog and fen species with high average *C* values. Our finding of significant differences in average *C* values by hydrogeomorphic type raises questions about the ability to distinguish "remnant natural plant communities" (sensu Swink and Wilhelm 1969) on soils that are subject to natural disturbance, as is the case with River-Influenced and Open-Coast Wetlands which are scoured by flowing water and waves. Although remnant natural plant communities would seem as likely to occur in high energy fluvial environments as they do in bogs and fens, *C* values may be a less reliable indication of whether or not such communities are natural remnants.

Plant Species in Relation to Water Depth

Water depth gradients are known to have an important effect on vegetation zonation, and depth zones are commonly used to partition Great Lakes wetlands prior to sampling (Geis 1979, Minc 1997, Burton *et al.* 2002). Our data confirm the importance of water depth to separating species in the environmental space depicted by the CCA plot (Fig. 3).

The inter-annual variability of lake levels has been a deterrent to developing vegetative indicators for Great Lakes coastal wetlands. Water levels in the Great Lakes vary on a range of temporal scales (Burton 1985, Trebitz *et al.* 2002), and water level changes influence the presence and extent of wetland vegetation (Stuckey 1975, Farney and Bookhout 1982, Geis 1979, Harris *et al.* 1977, 1981, Keddy and Reznicek 1986, Wilcox *et al.* 2002, Tulbure *et al.* 2007). Low lake levels probably influenced our data for Lakes Michigan and Huron, where average lake levels in July 2001 and 2002 were 42 cm below the long term average for the month (U.S. Army Corps of Engineers 2005), exposing extensive areas of lakebed in areas where bathymetry was gradually sloping. Consequently, a few of the indicator taxa for Open-Coast Wetlands were generalist species that colonize bare soil substrates by way of windblown seeds, such as *Salix petiolaris, Solidago canadensis,* and *Sonchus arvensis*. The later two taxa are facultative species that grow on uplands as well as wetlands (Reed 1988), and their determination as soil indicators in this study may be the result of our sampling during a low-water year.

Water level fluctuations may cause shifts in the geographic location of species, but should not shift species location in the environmental space represented by CCA axis 1 (Fig. 3). Although absolute water levels may shift over time as the Great Lakes rise and fall, the position of plant species relative to each other along a water gradient axis should remain constant: the submergent species that occupy the wet side of the water depth gradient will always occupy deeper water than the wet meadow species which occupy the dry side of the gradient.

The position of species relative to the tussock height axis in the CCA, however, may be a predictor of species that increase in abundance during low-water periods. Two of the species with the lowest values on the tussock height axis, *Juncus nodosus* and *Eleocharis erythropoda*, were more common in our study (30% and 23% of sites, respectively) than in a prior study by Minc (1997: 4.5% and 5.5% of transects, respectively) that sampled coastal wetlands when water levels in Lakes Michigan and Huron were higher than or near the long-term average. The more extensive distribution of these two species in our study versus that of Minc (1997) is likely due to establishment opportunities on sandy soils exposed during low lake levels in 2001 to 2003.

In general, our data on species frequency agree with those of Minc (1997), as 29 of the 36 most ubiquitous herbaceous zone species in the Minc study were on our common plant list. This agreement suggests that most species are minimally affected by natural fluctuations in Great Lakes water levels. Thus, indicators developed during a low lake level period could apply to periods of high lake level as well. This constancy may be partially due to the fact that most of the indicator species are perennials. Furthermore, many of the common plant species in our database have growth patterns that provide resilience to the stress of water level change, such as tussock formation (e.g., *Carex stricta*), floating mat formation (e.g., *Carex lasiocarpa*), and tolerance of widely ranging water depths (e.g., *Typha* spp.: Frieswyk 2005, Vaccaro 2005). Although the indicators presented here could be refined by repeat visits to our study sites during higher water periods, they provide a comprehensive basis for understanding of plant-environment relationships in Great Lakes coastal wetlands, which is an essential precursor for ecological condition assessments in such a large, heterogeneous region.

Physical Environment Indicators in Relation to Ecological Condition

A major challenge in the development of indicators of ecological condition is distinguishing the influence of natural variation from that of anthropogenically-induced environmental degradation. When developing a generic method to use plant species for assessing ecological condition, the results of the research presented in this manuscript could be used to filter out species that are uncommon and constrained to specific physical habitats. For example, species such as *Eleocharis quinqueflora, Proserpinaca palustris, Solidago uliginosa*, or *Triglochin maritimum*, which occurred in few plots and were strong indicators (i.e., high RA_{kj} values) of a particular soil type, would *not* make good candidates for development of a multi-species index of ecological condition because their absence would be more likely due to their specific habitat requirements and relative rarity in Great Lakes coastal wetlands rather than the effect of anthropogenic stressors *per se*. The results of this research might also be used to develop four separate multi-species indices of ecological condition for each of the four soil types, thus eliminating the potentially confounding variable of soil type at the onset of condition indicator development. Finally, the hierarchical partitioning of species variance among both physical and anthropogenic causes, as has been done by Brazner and colleagues (2007) for five wetland plant species, could be expanded to additional plant species using the results of this research as a basis to narrow the field of candidate species. Future work of this GLEI group will use this approach to develop ecological condition indicators with maximal responsiveness to anthropogenic stress.

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